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RAY TRACHEIDS IN ABIES

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(WITH PLATES XXIV AND XXV)

A characteristic feature of the Abietineae, as opposed to the remaining tribes of the Coniferales, is the possession of ray tracheids in their wood. To this statement exception must be made, on the one hand for the genera *Abies* and *Pseudolarix*, from which they have hitherto been regarded as quite absent, and on the other hand for a few species of the Taxodineae and Cupressineae, in which they have been reported to occur sporadically. Even in the latter, however, they never become normal features as in the Abietineae. This distribution has recently received two interpretations. PENHALLOW¹ held that in the species where they occur sporadically they are appearing for the first time, and from this condition develop to their culmination in the Abietineae. JEFFREY,² on the other hand, having observed their occurrence in association with a wound in *Cunninghamia sinensis*, regards their sporadic appearance as a reminiscence of an original abundant condition such as exists in the Abietineae. The application of these conflicting views in phylogenetic considerations of the whole family is obvious.

To the distribution briefly outlined above, the writer³ recently recorded an exception in the case of the genus *Abies*. In a wounded root of *A. amabilis* ray tracheids were discovered in considerable numbers. The only other record of their occurrence in the genus was made by PENHALLOW (*loc. cit.*), who observed them sporadically in *A. balsamea*. In view of the peculiar circumstances of their discovery and its bearing on the theories in vogue, it was considered advisable to investigate the material of *A. amabilis* fully and to examine other species of the genus.

The material in which the marginal tracheids were observed

¹ PENHALLOW, D. P., North American Gymnosperms. Boston. 1907.

² JEFFREY, E. C., Traumatic ray tracheids in *Cunninghamia sinensis*. Ann. Botany **22**:602. *pl.* 31. 1908.

³ THOMPSON, W. P., The origin of the ray tracheids in the Coniferae. Bot. Gaz. **50**:101-116. 1910.

consisted of a segment of a root several inches in length and containing about 25 annual rings. On one side a severe wound had been partially healed over. A photograph of a transverse section taken some distance above the wound is presented in fig. 1. Even at this low magnification, characteristic tangential series of traumatic resin canals may be observed in the 5th, 6th, 9th, and 12th annual rings. Therefore, the root must have been wounded at least four times. The repeated wounding had apparently sapped its vitality, for the later-formed annual rings were very narrow and infested with fungus filaments.

A more magnified view of one of the series of canals is shown in fig. 2. The arrangement is seen to be typically traumatic. In other respects the wood is of the normal *Abies* type.

A radial longitudinal section, taken at some distance from the outermost wound, is photographed at rather low magnification in fig. 3. Near the left of the figure the septated element and its neighbor on the right, which is also septated beyond the limits of the figure, form part of the traumatic series between the canals. Immediately on their right two ray tracheids are to be seen on the upper margin of the ray. The magnification is not sufficient to show the character of their pits except that they are smaller than those of neighboring wood tracheids.

The character of the pits on a similar element may be distinguished, however, in fig. 4, which is a photograph at a higher magnification of another section. Two of the pits in section on the extreme left are clearly bordered on the upper side and simple on the parenchyma side. The others, though not so clear, are likewise unilaterally bordered; therefore the long low element is a ray tracheid.

That interspersed as well as marginal tracheids are present is shown in fig. 5. The two pits on the conspicuous vertical end wall are distinctly bordered, as are those on the horizontal walls of the same cells. Therefore, these cells are ray tracheids occurring between the parenchymatous cells of the ray which are to be seen above and below. The parenchymatous cell below the ray tracheid is traversed by a filament of the fungus which probably gained entrance at the wounds.

Elongated ray tracheids of the type described by the writer (*loc. cit.*) as common in the young root of *Pinus* were also frequently observed. One of them is shown in fig. 9. The tail-like projection extends to the extreme upper right of the figure. A unilateral bordered pit may be observed in contact with the ray and a bilateral one in contact with a wood tracheid.

The figures just described show that ray tracheids of all kinds are present in this wounded root of *A. amabilis*. Normal material of the same species, root, stem, and branch was carefully examined, and, in accordance with all former observations, not a single ray tracheid found. Therefore, it must be concluded that those observed were in definite association with the wounds. In fact, their occurrence recalls precisely that described by JEFFREY for *C. sinensis*. Occurring, as they do, in one of the two abietineous genera which normally are entirely without them, their presence is all the more significant.

In JEFFREY's material of *Cunninghamia* the ray tracheids were found only on the side remote from the wound. In my material this was not the case, as they were often in direct contact with the traumatic canals. Of course, the position of the various traumatic series (see fig. 1) would indicate that the root had probably been wounded at different points on its circumference, and therefore even if JEFFREY's observation held good for this material, the ray tracheids ought to be found on any radius. However, in material of another species to be described immediately, such was distinctly not the case.

Let us now turn to the other species examined. A radial section of a wounded branch of *A. concolor* is shown in fig. 7. The short septated elements at the central part of the extreme left are part of the traumatic series. Following these on the margins of both rays are bordered-pitted elements which are obviously ray tracheids. The conditions existing in the wounded root of *A. amabilis* are thus exactly duplicated in the wounded branch of *A. concolor*. In both species the ray tracheids are often in line with parenchyma cells, as in fig. 7. The usual condition is the appearance of one or two parenchymatous cells in the summer wood and a similar number of ray tracheids conterminous with them in the first-formed spring

wood of the following year. Between these and the summer wood of the same year neither kind of element is to be found.

Another species in which ray tracheids were found is *A. homolepis*. Fig. 8 shows a ray in the region of the annual ring. On the upper margin are ray tracheids in line with a parenchyma cell. Fig. 12 is a more magnified view of these elements, and shows the bordered character of the pits more distinctly, especially of the two on the end wall. The material of *A. homolepis* is particularly interesting from the fact that it exhibited no trace of wounding either in radial or transverse sections. As the segment was of considerable length and contained ray tracheids throughout, the presence of the latter could scarcely have been the result of a distant wound, especially as there was no trace of traumatic canals. Their presence, therefore, must be considered as normal, or at least sporadic.

The only other species in which these structures were observed is *A. Veitchii*. Fig. 11 demonstrates their presence in this form, the bordered pit on the end wall being most distinct. The material was similar to that of *A. homolepis*, a branch which showed no trace of wounding. As in the other species, their typical position was in the spring wood following one or two parenchymatous cells in the summer wood of the previous year (see fig. 11).

Many other species were examined, including *A. lasiocarpa*, *Fraseri*, *Nordmanni*, *cephalonica*, *grandis*, *balsamea*, and *firma*, but none were found to have ray tracheids. A very diligent search was made in the case of *A. balsamea*, in which PENHALLOW reports having observed them sporadically. Normal and wounded roots, stems, branches, and seedlings, as well as witches' brooms, all failed to show a single indisputable ray tracheid. However, material collected during the active growing season and examined in the cambial region showed a slight border on the pits of some of the cells, which from their position were evidently doomed to degeneration in a manner to be described below.

In all those species in which ray tracheids were found, their position and association with neighboring cells were very suggestive. As has been described, they usually occurred in the spring wood, and were conterminous with one to several parenchyma

cells in the summer wood of the previous year (figs. 7, 8, 11). These groups of parenchyma cells at the boundary of the annual ring are characteristic features of many species of *Abies*. In the spring wood they disappear, to be revived again in the following summer wood. The result is the appearance of single cells or small groups of cells scattered along the margins of the rays, each group at the end of an annual ring. Between the groups there is usually no trace of cells, but here and there peculiar "ghostlike" appearances resembling cells may be seen. One of them is shown in fig. 6, which is a photograph of a section of *A. homolepis*. They are shadowy, structureless affairs, staining best in hematoxylon and giving no response to the phloroglucin test for lignin. Occasionally they form an almost continuous cell-like series from one group of parenchyma cells to the next, but usually they are rather isolated. That these structures are not merely thin sections of the sides of actual living cells is shown by their staining qualities, by their lack of structure, and by a study of a series of sections. The only explanation for their presence is that they are degenerated cells. In fact, it is possible to observe, especially in the cambial region, all stages in degeneration from such a conspicuous object as that seen in fig. 6, to ones which are barely discernible even with the strongest staining. The scattered condition is obviously due to the complete disappearance of some members of the series.

Now when ray tracheids occur, they identify themselves definitely with these series of degenerating cells. They may often be observed conterminous with one of the "ghosts." The inference seems irresistible that these "ghosts" were originally complete rows of ray tracheids which have degenerated in most species, but may survive sporadically in a few, and may be recalled traumatically in others.

The groups of parenchyma cells at the end of the annual ring are likewise definitely identified with these degenerating cells, whether ray tracheids are present or not. It seems probable that at the end of the year's growth, when there is a great demand for storage in preparation for the approaching winter, the cells which would otherwise degenerate are given a new lease of life and transformed into parenchyma cells which are capable of storage. That

the transformation has actually taken place is proven by the discovery of intermediate forms of cells. In fig. 10, which is a more magnified view of the lower part of fig. 8, is an element with a distinct bordered pit on its vertical wall and several equally distinct simple pits on its horizontal wall. This element, therefore, is neither a tracheid nor parenchyma cell, but combines the pitting of both. Several such cells were seen, in some cases both kinds of pits occurring on the same wall. So far as the writer is aware, the anomaly of bordered and simple pits occurring on the same element has never been observed except in this laboratory by Miss GORDON⁴ in material of *Sequoia*.

A much commoner type of transitional element than the anomalous structures just described is illustrated in fig. 13, from *A. Veitchii*. The pits on the ray tracheid are so slightly bordered as to be scarcely distinguishable from the simple pits of the parenchymatous cells. The figure illustrates but one or two of the many forms intermediate between typically simple and typically bordered pits which may be observed on these elements.

Conclusions

The presence of ray tracheids as a result of wounding in *A. amabilis* and *A. concolor* parallels exactly the phenomena described by JEFFREY for *C. sinensis*. The interpretation advanced by him is that we have here a case of the revival by wounding of structures ancestrally present and lost in the course of evolution. Owing to the closer affinity of *Abies* with those genera in which ray tracheids are abundant, his reasoning applies with even greater force to the observations described in this paper. Again, their sporadic occurrence in uninjured material of a few species of the genus strongly supports this view. Further support is added by the association of the ray tracheids with the degenerating cells or "ghosts," and with the groups of marginal parenchyma cells at the ends of the annual rings. It may be concluded that ray tracheids were present in the ancestors of *Abies*, and have per-

⁴ GORDON, MARJORIE, Ray tracheids in *Sequoia sempervirens*. New Phytol. 11:1-7. figs. 7. 1912.

sisted sporadically in a few species, but in the majority have either degenerated or been transformed to parenchyma.

Summary

1. Ray tracheids, marginal, interspersed, and elongated, were observed in association with wounds in *A. amabilis* and *A. concolor*.

2. They were also observed in uninjured material of *A. homolepis* and *A. Veitchii*.

3. Their usual position was in contact with a series of degenerated cells on one hand and a group of parenchyma on the other.

4. Transitions from ray tracheids to parenchyma were common, some elements having both bordered and simple pits, and others pits with borders of various sizes.

5. All the evidence points to ray tracheids being present in the ancestors of *Abies* and absent today by reduction.

The writer is indebted to Professor C. S. SARGENT for permission to collect material in the Arnold Arboretum, and to Mr. R. B. THOMPSON for material and advice. The work was carried on under appointment as an "1851 London Exhibition Science Research Scholar" of the University of Toronto.

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EXPLANATION OF PLATES XXIV AND XXV

PLATE XXIV

FIG. 1.—*Abies amabilis*: transverse section of wounded root, showing several series of traumatic resin canals; $\times 12$.

FIG. 2.—The same: higher magnification, showing a row of traumatic resin canals; $\times 100$.

FIG. 3.—The same: radial section; $\times 150$.

FIG. 4.—The same: radial section, showing marginal ray tracheid with bordered pits in section; $\times 800$.

FIG. 5.—The same: interspersed ray tracheid; $\times 1200$.

FIG. 6.—*Abies homolepis*: radial section, illustrating the presence of "ghostlike" degenerated cell; $\times 400$.

PLATE XXV

FIG. 7.—*Abies concolor*: radial section, showing wound tissue on the left and ray tracheids on the margin of both rays; $\times 500$.

FIG. 8.—*Abies homolepis*; showing marginal ray tracheids; $\times 600$.

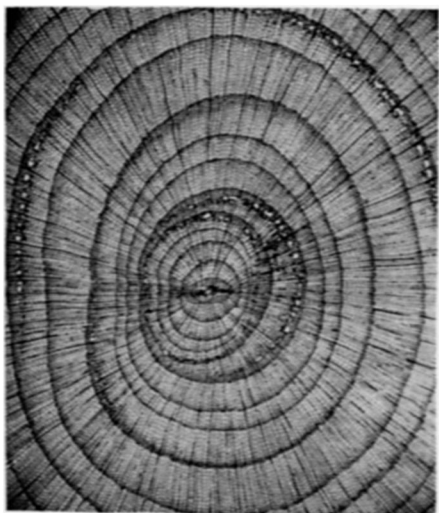
FIG. 9.—*Abies amabilis*: showing vertically elongated ray tracheid; $\times 800$.

FIG. 10.—*Abies homolepis*: showing element with both bordered and simple pits; $\times 800$.

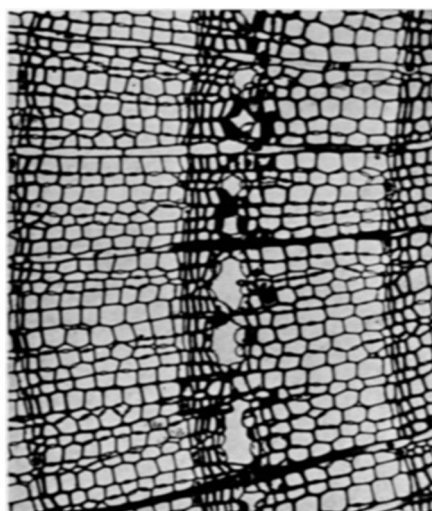
FIG. 11.—*Abies Veitchii*: showing presence of ray tracheid conterminous with parenchyma cell; $\times 600$.

FIG. 12.—*Abies homolepis*: high power to show ray tracheid; $\times 1000$.

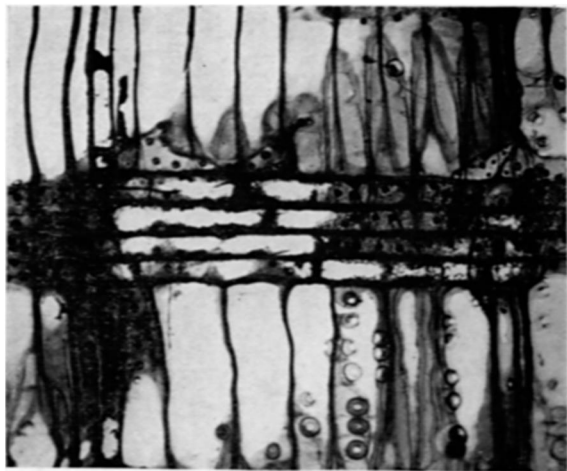
FIG. 13.—*Abies Veitchii*: an element with pits very slightly bordered; $\times 600$.



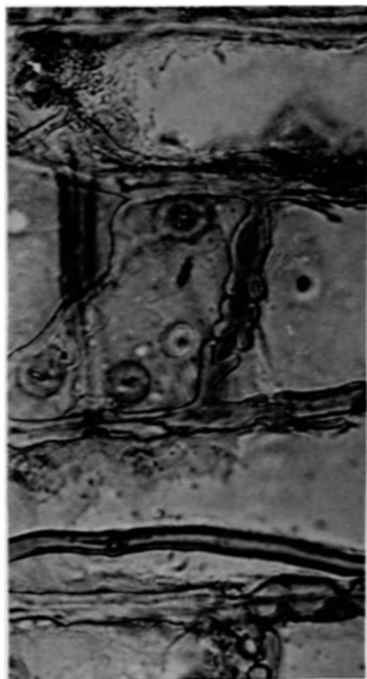
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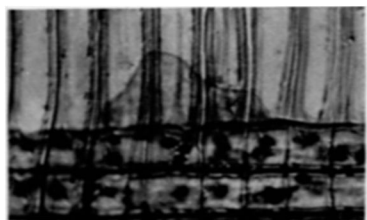
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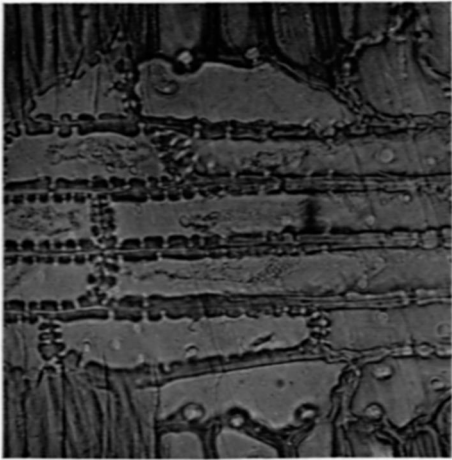
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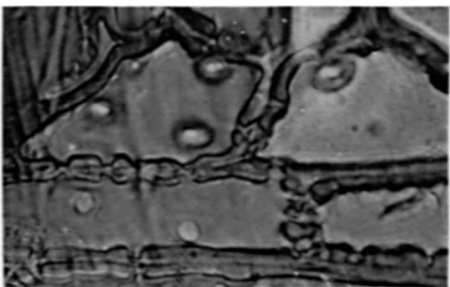
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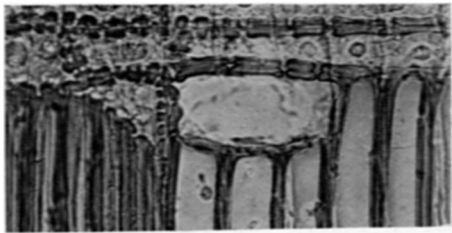
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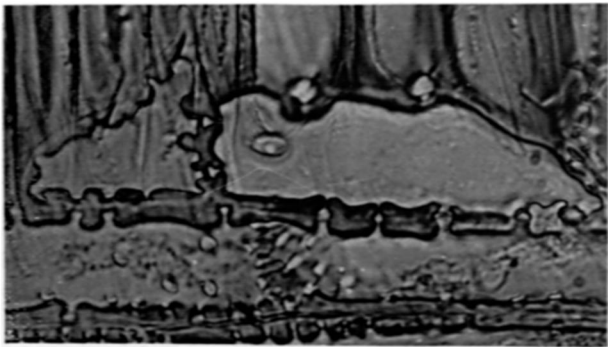
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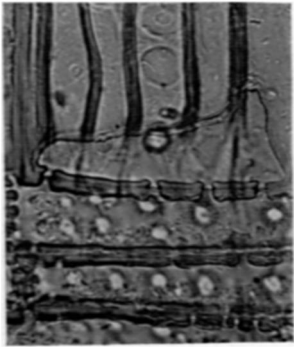
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